THE STATUS OF THE GENERA AMPHIPAPPUS, AMPHIACHYRIS, GREENELLA, GUTIERREZIA, GYMNOSPERMA AND XANTHOCEPHALUM (COMPOSITAE)

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The taxonomic status of the genera *Amphipappus*, *Amphiachyris*, *Greenella*, *Gutierrezia*, *Gymnosperma* and *Xanthocephalum*, has been questioned recently by L. Shinners (1950). Since other authors (Torrey and Gray 1841, Bentham and Hooker 1873, Hoffmann 1890, Gray 1884, Rydberg 1917) have disagreed as to the treatment of these genera, it was thought to be of interest to reevaluate their position.

Previous investigations were based largely on superficial morphological observations. In attempting to treat the problem in a more objective fashion, a more detailed cytological and morphological study has been attempted. This has been by no means exhaustive, but the new data offer, in the author's opinion, sufficient information to delimit these genera satisfactorily.

CONCEPT OF GENUS AND ITS RELATIVE VALUE

To give a definition of a genus is as hard a problem as to try to define a species and no attempt will be made to solve this problem here. Nevertheless, a few considerations might be pertinent to the problem under consideration. They also will illustrate the author's ideas about these matters and the underlying principles of this work.

A genus is formed by a group of species which share a series of common properties. It is also related to other genera by some common properties, so as to allow us to place them in a particular tribe, subfamily or family. There is no fixed set of rules that determines which characters will be of "generic" and which of "specific" value, but we may say that if the common properties a group of species share are greater than the properties this group shares with another set of species (viz. another genus), we usually place these two groups of species in different genera. On the other

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hand if the species of the first group resemble those of the second group as much as each other, we usually place them in the same genus.

When the first case applies, that of a group of species resembling each other more than species of another group, we still might maintain them in the same genus, but in different subgenera or sections. This last procedure will be largely determined by the author's concept, and is therefore somewhat subjective. Also, it is likely to be influenced by the traditional usage in the family.

In the Compositae the tendency has been to erect many genera based on a few characters. The desirability of this could be disputed, but it has to a certain extent had a very practical basis. In a family as large and as homogeneous as this one, it is very hard to obtain a good understanding of large genera, e. g. *Senecio*, *Haplopappus*, *Baccharis*, *Solidago*, etc., while smaller groups (which are not necessarily always too small) can be better understood.

HISTORY OF THE GENERA UNDER STUDY

Xanthocephalum, with one species *X. centauroides*, was the first genus of this group to be described, in 1806, by Willdenow. The very brief description indicates only that the genus "belongs close to *Zoegea*"[2]

Lagasca (1816), in his original description of *Gutierrezia*, did not indicate its relationship to other genera. Nuttall (1818) indicated in his description of *Brachyris* (= *Gutierrezia*) the possesion of "vegetation almost similar to that of *Euthamia tenuifolia*". Both authors state that the involucre is formed by imbricated bracts, the heads are radiate, and the pappus paleaceous. However, all of these characters occur in several genera of Astereae, and therefore are not sufficient by themselves to define *Gutierrezia*.

The genus *Gymnosperma* was described by Lessing in 1819 based on *Selloa glutinosa* Spreng. Since *Selloa* H. B. K. a later name for another Mexican plant was conserved, *Selloa* Spreng. becomes a rejected name, and *Gymnosperma glutinosum* Less. is the correct name for the plant (Blake, 1930; Int. Rules Bot. Nom., Ap. III, Sect. X, 9168). Lessing states no relationships, other than the "undoubtedly asteraceous character" of the genus.

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[2] "Eine zur Syngenesia frustranea gehörige Gattung, die bei *Zoegea* stehen muss".

De Candolle (1836) defines *Brachyris* Nutt. (= *Gutierrezia*) according to its habitat, the number of ligulate and tubular flowers, the form of the inflorescence, and the pappus, which is formed by well developed paleae of moderate size. He placed it near *Gymnosperma* Less., which has a pappus of very minute teeth, and *Hemiachyris* D. C., a genus with one species in De Candolle's conception, *H. texana*, which differs from *Gutierrezia* in having a pappus of short paleae in the tubular flowers and none in the ligulate ones.

Nuttall (1841) elevated *Amphiachyris*, considered by De Candolle to be a section of *Gutierrezia* (*Brachyris*), to generic rank. The principal justification was given as the following constellation of characters: "the involucrum obovate and bracteolate, scales few and obtuse not herbaceous at the points", and the "pappus of the discal florets united at base, dividing into about six entire setae. Radial florets with a very minute crown of scarcely visible setae".

Torrey and Gray (1841) accepted Nuttall's treatment of *Amphiachyris* but reduced *Hemiachyris* D. C., to become a section of *Gutierrezia*, a step which has been accepted by all later workers. They placed *Gutierrezia* next to *Gymnosperma* and *Amphiachyris*, from which it differs by the pappus characters already cited, and next to *Brachychaeta*, which differs from the above mentioned genera by its setiform pappus.

Bentham and Hooker adopted a more conservative attitude in the Genera Plantarum (1873). They merged both *Hemiachyris* and *Amphiachyris*, as well as the quite distinct genus *Amphipappus*, which had been described by Torrey and Gray in 1845 from material collected by Fremont in California, with *Gutierrezia*. This complex was then placed near *Gymnosperma* and *Xanthocephalum*, which differ from *Gutierrezia* in lacking a paleaceous pappus. In addition, *Gymnosperma* differs by its possession of minute ligules instead of well developed ones as in the other genera, and *Xanthocephalum* by its broad involucre. Also, *Grindelia* is considered to be very close, differing mainly in the shape of the involucre and involucral bracts.

In the Synoptical Flora (1884), Gray adopted a point of view close to that which he had held in 1841, the main difference being the transfer of *Amphipappus fremontii* into

Amphiachyris. Hoffmann's treatment (1890) for Engler's Pflanzenfamilien is similar to that of Bentham and Hooker (1873).

Most authors of local or regional floras in the United States have followed Gray's views as expressed in his Synoptical Flora. Exceptions to this are Rydberg's Flora of the Rocky Mountains (1917), in which this author restores *Amphiachyris fremontii* to *Amphipappus* T. & G.; and Blake (1924) who accepted *Amphipappus fremontii* but considers *Amphiachyris dracunculoides* to belong to *Gutierrezia*.

Porter (1943) reviewed *Amphipappus* and effectively established its status as a separate genus.

A radically different point of view has recently been adopted by Shinners (1950), who merges *Gutierrezia*, *Gymnosperma*, *Amphiachyris* (including *Amphipappus*), and the heterochromous *Greenella* Gray, all under *Xanthocephalum*. For Shinners, "the quite variable features of pappus, size of heads, and number of rays" do not constitute differences sufficient to justify the maintainance of separate genera.

CYTOLOGICAL AND MORPHOLOGICAL OBSERVATIONS

CYTOLOGICAL STUDIES. An attempt has been made to determine the basic chromosome numbers of as many species as possible of all the genera under consideration, as well as those of other more or less related genera in Astereae-Solidaginae. Part of these data have been published elsewhere (Raven, Solbrig, Kyhos and Snow, 1960) and part are presented here.

Table 1 shows the chromosome numbers of species of *Gutierrezia*, *Amphipappus*, *Amphiachyris*, *Xanthocephalum* and *Gymnosperma*. Unfortunately, only one species of *Xanthocephalum* and none of *Greenella* could be counted. Each of these genera studied proved to have a different basic chromosome number: four in *Gutierrezia*, five in *Amphiachyris*, six in *Xanthocephalum*, seven in *Gymnosperma* and nine in *Amphipappus*. The chromosome number thus proved to be an absolute distinguishing character between the genera. It can also be seen how the chromosome number con-

TABLE 1. CHROMOSOME NUMBERS

Species	n	2n	No. of counts	Reference
Amphiachyris dracunculoides	5	10	2	Solbrig, 1959
Amphipappus fremontii	9	—	2	Raven, Solbrig, Kyhos and Snow, 1960
Gutierrezia texana	4	—	3	Solbrig, 1959
Gutierrezia glutinosa	4	—	2	Solbrig, 1959
Gutierrezia serotina	4	—	1	Solbrig, 1959
Gutierrezia sarothrae	4, 8	8	20	Solbrig, 1959
Gutierrezia microcephala	8, 16	—	6	Solbrig, 1959
Gutierrezia bracteata	8, 12	16, 24	10	Solbrig, 1959
Gutierrezia californica	12	—	1	Solbrig, 1959
Gymnosperma glutinosum	7	—	1	Solbrig, 1959
Xanthocephalum gymnospermoides	6	12	2	Solbrig, 1959

firms *Gutierrezia (Hemiachyris) texana* as a true *Gutierrezia.*

MORPHOLOGICAL STUDIES. — **Involucre.** The shape of the involucre can be used in delimiting the genera under consideration, but it is not sufficient by itself in certain cases.

Gutierrezia possesses a characteristic elongate-turbinate involucre which varies from slightly campanulate in *G. glutinosa* and broadly turbinate in *G. texana* to narrowly elongate-turbinate in *G. microcephala.* The involucres of *Amphipappus* and *Gymnosperma* do not differ essentially from that of *Gutierrezia.* In contrast with them, *Xanthocephalum, Amphiachyris,* and *Greenella* have broadly campanulate involucres. Of these last three genera, *Amphiachyris* has an involucre most similar to that of *Gutierrezia glutinosa* to the point that in some cases only close observation

permits their separation on this basis. The involucre of *Xanthocephalum*, on the other hand, is quite different and very similar to that of *Grindelia*, a genus similar to *Xanthocephalum* in habit and chromosome number. *Greenella* possesses an almost hemispherical involucre, which may be easily distinguished from that of all species of these genera with the exception of *Gutierrezia glutinosa* and *Amphiachyris dracunculoides*.

Involucral bracts. There is little variation in the involucral bracts, whether within or between genera. The bracts are herbaceous with a hyaline margin and a dark green tip. The involucral bracts of *Xanthocephalum* are a little darker in color than those of the other genera.

Pappus. The characters of the pappus, which were used by the very first botanists in the study of these genera, are very valuable, although not necessarily absolute, criteria for delimiting them.

In order to use the pappus characters successfully one must consider the pappus of both ligulate and tubular flowers and the variation present in different species.

In fig. 1 are depicted pappus scales and bristles characteristic of the different genera under consideration. *Gutierrezia* has the most distinctive and characteristic pappus of the group. Both ligulate and tubular flowers have a well developed pappus formed by lanceolate paleae, with a slightly fimbriate margin. The paleae of the ligulate flowers are usually slightly shorter; in *G. texana* they are absent or very reduced, a characteristic used by De Candolle in establishing the genus *Hemiachyris*. The paleae are about the same size as the achene except in *G. texana* and *G. glutinosa*, where they are shorter than the achene. In no case are they longer than the corolla (for a detailed analysis of the variation of this character in *Gutierrezia*, see Solbrig, 1959).

Amphipappus has numerous, linear, toothed, pappus-setae, which are slightly longer than the tubular corollas. They are sufficiently distinct to characterize the genus, as already noted by Asa Gray (1873). *Gymnosperma* and *Greenella* are similar in possessing a reduced crown of minute scales instead of a well developed pappus, in both ligulate and tubular corollas.

Xanthocephalum usually has only a low rim or crown in both ligulate and tubular corollas. It is not uncommon, however, to find in some or all of the tubular flowers of every species, one to three elongated, triangular-shaped, irregular awns.

Amphiachyris usually has no pappus at all in the ligulate flowers, or only a low, scaly ring. However, the tubular corollas, possess a pappus of few, ephemeral, dilated bristles

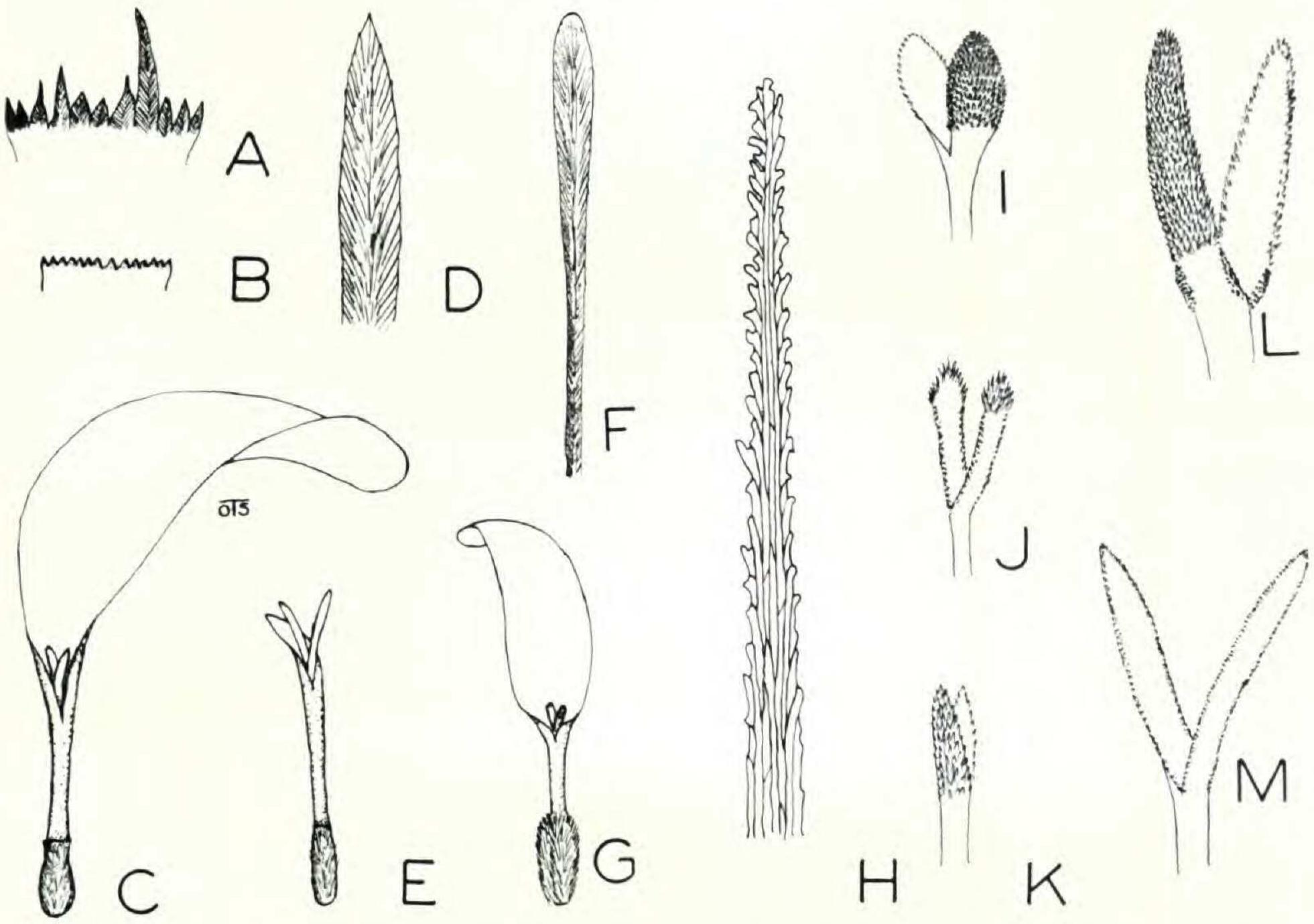

FIG. 1. *Xanthocephalum gymnospermoides: A.* Pappus × 5; *J.* Style of tubular flower × 16. *Xanthocephalum wrightii: C.* Ligulate flower × 2. *Gymnosperma glutinosum: B.* Pappus × 5; *E.* Ligulate flower × 2. *Gutierrezia sarothrae: D.* Pappus bristle × 5; *L.* Style tubular flower × 16. *Amphiachyris dracunculoides: F.* Pappus bristle × 5; *K.* Style tubular flower × 8. *Amphipappus fremontii: G.* Ligulate flower × 2; *H.* Pappus bristle × 5; *I.* Style tubular flower × 8; *M.* Style ligulate flower × 16.

which are fused at the base. There is some variation, with the bristles sometimes broad enough to resemble the characteristic paleae of *Gutierrezia*. This resemblance is nevertheless more apparent than real.

Corolla. The tubular corollas are essentially alike. The ligulate corollas manifest some significant differences in a few instances.

Gymnosperma has ray flowers with ligules which do not surpass the tubular corollas. In all the other genera the ray

corollas are bigger than the tubular ones. The ligules of *Xanthocephalum* are larger and more numerous than those of the other genera. *Greenella* is the only genus of the group with white ligules, all the other genera having yellow ones.

Anthers and pollen. The anthers are essentially alike in all the genera under consideration. Their shape is characteristically asteraceous, with a blunt base and a more or less triangular, rounded connective. The pollen is also very uniform in all the genera and is also of the characteristic type for the tribe.

Styles. The variation in styles is not very great from genus to genus; nevertheless, in certain cases the differences are significant enough to deserve attention, especially since classical synantherologists have attributed so much importance to characters of the styles in the delimitation of tribes and genera of Compositae (Bentham 1873).

The styles of the female ray flowers are different from those of the hermaphrodite tubular ones. We find in the ray flowers a style composed of two elongated branches, gradually attenuated toward the tip and with a border of papillae along both sides of the stigmatic branches. This situation holds true for all the genera considered here.

The branches of the style of the tubular flowers are shorter than those of the ligulate ones. In addition, instead of having the stigmatic papillae all around the border of the two stigmatic branches, they are confined to the lower quarter on both sides. Finally, both external sides of the stigmatic branches are covered with collecting hairs.

The collecting hairs may be well developed and pointed as in *Gutierrezia*, *Xanthocephalum*, *Greenella*, and *Amphiachyris*, or they may be slightly smaller and with rounded tips as in *Amphipappus* and *Gymnosperma*. These two genera also have elliptic rather than subulate style branches.

Stigmatic papillae are totally lacking in the tubular flowers of *Amphipappus fremontii* and *Gutierrezia microcephala*. In *Xanthocephalum gymnospermoides* the papillae extend beyond the middle of the stigmatic branches, while the collecting hairs are restricted to the upper part of the style (fig. 1). These variations have, nevertheless, only specific value.

TABLE 2. PRINCIPAL DIFFERENTIATING CHARACTERS

	GUTIERREZIA	AMPHIACHYRIS	XANTHOCEPHALUM	GYMNOSPERMA	AMPHIPAPPUS	GREENELLA
Basic chromosome no.	4	5	6	7	9	
Involucre	turbinate	campanulate	campanulate	turbinate	turbinate	campanulate
Pappus ligulate fl.	paleae	minute	minute	minute	minute	minute
Pappus tubular fl.	paleae	setae	minute and or squamellae	minute	setiform paleae	minute
Ligules	less than 15 medium-sized yellow	10 to 20 medium-sized yellow	more than 20 large yellow	less than 10 very short yellow	less than 10 medium-sized yellow	10 to 20 medium-sized white
Stigma branches	subulate	subulate	subulate	elliptic	elliptic	subulate
Collecting hairs	pointed	pointed	pointed	blunt	blunt	pointed
Habit	perennial or annual	annual	annual	perennial	perennial	perennial or annual
Blooming time	Fall	Fall	Fall	Fall	Spring	Fall

HABIT AND DISTRIBUTION

Amphipappus is the only spring-blooming genus of the group. It is a suffrutescent perennial shrub restricted to the regions of the Colorado River basin in southern Utah, Nevada and South-east California (Porter, 1943). The author's observations on one population near Shoshone, California, show that leaves and small branches die out entirely during the dry season. Unfortunately, this condition could not be confirmed for plants in the greenhouse, since they died shortly after blooming.

Xanthocephalum is a genus of annual, fall blooming plants, mostly from central Mexico (Matuda, 1958). Two species, *Xanthocephalum gymnospermoides* and *X. wrightii*, reach the mountains of southern Arizona and New Mexico, growing at elevations of 800 to 2,500 meters.

The number of species of *Greenella* is probably three. They are also mainly Mexican, growing on Cedros Island, Baja California, and in northern mainland Mexico and southern Arizona. They are perennial, fall-blooming plants, with the exception of the annual *G. arizonica*.

Gymnosperma glutinosum, the only member of the genus, ranges from northern Guatemala to Arizona, New Mexico and Texas. It is also perennial and fall-blooming.

Amphiachyris, as here delimited, has two species, *Amphiachyris dracunculoides* (DC.) Nutt., and *Amphiachyris amoenum* (Shinners) Solbrig[3]. Of these two annual, fall-bloomers, *A. dracunculoides* has apparently spread from its native habitat in Oklahoma and Texas throughout the dry parts of the Great Plains as far north as Kansas and Illinois and eastward into Kentucky and Louisiana. Nevertheless, it is considered to be a weed of only secondary importance. *Amphiachyris amoenum*, on the other hand is not common, being restricted to limestone soils of the Grand Prairie and eastern Edwards Plateau (Shinners, 1951).

Gutierrezia is the most widely distributed of this group of genera. It is found in western and central North America scattered in dry and rocky areas west of the central plains and reaching from Alberta and British Columbia in the north, to San Luis Potosi, Mexico, in the south. It is also

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[3] *Amphiachyris amoenum* (Shinners) comb. nov., based on *Xanthocephalum amoenum* Shinners Field and Lab. **19**: 77, 1951.

found in South America, namely in south western Bolivia, northwestern Argentina and northern Chile. It prefers loose, sandy soils. The species are either globose perennial shrubs or stout annuals, these latter being restricted to northeastern Mexico, New Mexico, Texas and Oklahoma (Solbrig, 1959).

KEY TO THE GENERA

A. Ray corollas equaling or shorter than the tubular corollas ..... 1. GYMNOSPERMA.

AA. Ray corollas longer than tubular corollas.

B. Pappus of both ligulate and tubular flowers composed of several well developed paleae (lacking in the ray of *G. texana*) ..... 2. GUTIERREZIA.

BB. Pappus of both ligulate and tubular flowers composed of setae, or low toothed crown, or lacking.

C. Involucre turbinate, appressed; perennial spring-blooming shrubs ..... 3. AMPHIPAPPUS.

CC. Involucre campanulate; perennial or annual fall-blooming shrubs or herbs.

D. Perennial (Except *G. arizonica*); ligules white ..... 4. GREENELLA.

DD. Annuals; ligules yellow.

E. Rays more than 20; pappus of tubular flowers reduced to a crown of minute scales or with 2 or 3 squamellae ..... 5. XANTHOCEPHALUM.

EE. Rays less than 20; pappus of tubular flowers of few ephemeral setae fused at base ..... 6. AMPHIACHYRIS.

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